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**FURTHER INVESTIGATION OF THE TRANSMISSION
OF ARBITRARY ENVIRONMENTAL INFORMATION
BETWEEN BOTTLE-NOSE DOLPHINS**

University of California, Davis
for the
Research and Engineering Department
San Diego, California
December 1968

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Technical Director

This study is one in a series being conducted by the Naval Undersea Warfare Center on dolphins. It describes the capacity of the acoustical signaling system of bottle-nose dolphins to transmit information about an arbitrary environmental event.

The study was conducted under the direction of Jarvis Bastian, Ph. D., Department of Psychology, University of California, Davis, under contract number N123(60530)57196A issued by the Naval Undersea Warfare Center. The work was completed and the results submitted in September 1968. The text is reproduced here in the format used by the contractor.

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FURTHER INVESTIGATION OF THE TRANSMISSION
OF ARBITRARY ENVIRONMENTAL INFORMATION
BETWEEN BOTTLE-NOSE DOLPHINS

by

J. Bastian
C. Wall
C. L. Anderson

University of California, Davis
for the
Research and Engineering Department

PROBLEM

Establish the critical signal characteristics of sounds emitted and received by a pair of bottle-nose dolphins during a test of their capacity to transmit information concerning the arbitrary features of their environment. Investigate the nature of the behavioral processes involved in the sound emission and reception.

RESULTS

The signals successfully used by the dolphins to transmit information in the tests were apparently the result of specific learning that occurred during the training period leading up to the actual information-transfer tests. No evidence was found to support the supposition that the social signaling of dolphins is capable of the transfer of arbitrary environmental information.

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INTRODUCTION

In our previously reported investigations* of the capacity of bottle-nose dolphins for the social transmission of information concerning arbitrary features of their environment, we had obtained clear evidence of very effective information transfer of this kind from a highly simplified experimental situation.** We had also been able to report considerable evidence concerning the nature of the signals by which this information was transferred, but we had not been able to clearly establish the critical signal characteristics. We had also not been able to resolve some of the important issues concerning the nature of the behavioral processes involved in the emission and effective reception of these signals, particularly with regard to whether the animals' success was attributable to the semantic capacities of the social communications of these animals or whether it was instead the product of more restricted features of their response to this specific experimental situation. The work discussed in the present report was undertaken to obtain experimental information bearing on these problems.

*Bastian, J. The Transmission of Arbitrary Environmental Information Between Bottle-Nose Dolphins. U.S. Naval Ordnance Test Station, TP 4117, 1967; also published in much the same form in N.A.T.O. Advanced Study Institute on Animal Sonar Systems, Biology and Bionics, R.-G. Busnel (Ed.), Laboratoire de Physiologie Acoustique, INRA-CNRZ, Jouy-en-Josas, France, 1967, Vol. II, pp. 803-873.

**The previous work involved an investigation of the capacity of a pair of bottle-nose dolphins to perform a cooperative task which required the acoustical transmission of information about an arbitrary visual event in the environment of one of the animals. Each animal was first trained to press one of two paddles, depending upon the state of a light signal. Next, while housed in adjacent enclosures, they were required to coordinate their actions in a fixed sequence and within fixed time limits. Then the light signal to the animal required to respond first was removed, and visual contact with the other animal and its light was eliminated. The pair continued to perform successfully as long as they were in acoustical contact and the light signal to the one animal was provided.

OVERVIEW OF THE PRINCIPAL EXPERIMENTS AND THEIR RESULTS

This report is most conveniently presented in terms of the chronological phases in which the work was conducted, as each was rather specifically addressed to one or the other of the aforementioned problems. These different phases of the investigation will be designated in what follows as Retraining, Playback Experiment I, S^D Reversal Training, Playback Experiment II, and Role Reversal, and will be briefly described now to provide an overview of the work and its main results.

RETRAINING

In the retraining phase we were concerned to reestablish the behavior capabilities of the animals who had not worked on the experimental task in the long period during which the procedures for analyzing the animals' signals were being developed and applied to the immense amount of material that had been recorded from the previous work. By gradually reintroducing the animals to the information transfer testing situation, using the original procedures, we hoped to be able to exploit our previously acquired information on the nature of the signaling system to retrace the development of the signaling actions, for we had not been equipped to discern its original development when both the animals and we ourselves were naive. We also hoped by watching its redevelopment to obtain a clearer understanding of the critical components of the signaling system. These hopes were realized though, it must be confessed, mostly because the animals gradually changed their system of information transfer to make it much simpler.

PLAYBACK EXPERIMENT I

The Playback Experiment was designed to help us more completely characterize by direct behavioral tests the critical signal attributes. This was to be achieved by presenting to the male animal, who was the recipient of the information supplied by the female, reproductions of recordings of the female's signals. The reproductions could then be manipulated in various ways to determine restrictions on the effectiveness of the signals in controlling the male's behavior. Unfortunately, the goals of this Playback Experiment could not be reached, at least partly because of technical deficiencies in our equipment which did not permit a clean reproduction of the recorded signals. Though it appeared that the male could have been brought to distinguish features

in the reproduced signals to perform appropriately, that is, he could have learned to discriminate what was presented to him, we decided to terminate the experiment because of the lack of easy interchangeability between recorded and original signals and because of the hope that better equipment would be available following the next phase of the work to permit better testing of the playback experimental possibilities.

S^D REVERSAL TRAINING

In order to further probe the behavioral processes underlying the female's signal emissions as well as to more closely determine the semantics of her signals, the animals were exposed to new experimental conditions in which the light source (S^D) which had previously indicated that one paddle was the appropriate one to press now was associated with the other paddle condition. The reversal was first effected abruptly but as it soon appeared that their overall behavior patterns might be lost before they adjusted to the changed condition the animals were then introduced to the reversed S^D conditions separately through the same program of training as had been followed in the original training and retraining. The signaling actions the female produced when then re-exposed to the necessity to transmit information about the S^D condition enabled us to answer, quite firmly in the negative, a number of questions concerning the appropriateness of interpreting the observed information transfer in terms analogous to human linguistic transactions. It was found that the relation of the contrasting features of her signals to the S^D light condition remained unchanged. Thus the semantic content of the signals she emitted was equivalent to "The light is X" or "The light is not X" rather than to instructions to press a particular paddle. Furthermore, the changes in her signaling actions occurring while she was undergoing S^D reversal training, when alone in the tank and when later joined by the male under increasing degrees of visual isolation, strongly indicate that her signaling actions had originally been adventitiously conditioned as part of her response to the S^D lights during the course of the initial visual separation as a consequence of the differential results with which these phonatary actions became associated in the male's actions. There was no evidence to indicate (and much to contra-indicate) that the animals' performance success had derived in any direct way from their "normal" modes of social interaction. The results thus contradict any supposition that the social signaling of these animals departs from typical mammalian patterns of social communication in their semantic aspect, particularly in the direction of human languages.

PLAYBACK EXPERIMENT II

During the final stages of the preceding experiment, a series of critical acoustical and video recordings of the female's actions were made in preparation for a second attempt to test the playback experimental possibilities for controlling the male's actions, this time with what we hoped would be more accurate, and thus potentially more effective, reproduction of the recorded signals made possible by the use of a better transducer for delivering the recorded signals into the water. However, these hopes were again unrealized; the signals, as reproduced, could not be used to control the male's paddle actions in place of the female's actual signal emissions. But there were reasons for our continuing to think that this failure was due to inadequate reproduction of the signals, for we had not eliminated in either this attempt or in the first playback experiment the switching transients which developed in the control circuitry. (We plan to make still another attempt to develop the capability for running the playback experiment, not only for the purposes of the present study, but also because of the great value the possession of a system for reproducing behaviorally effective recordings of these animals' acoustic signals would have for many other research purposes.)

ROLE REVERSAL EXPERIMENT

The last phase of the work reported here, which is as yet not completed, was undertaken to provide additional information of importance to the interpretation of the animals' success obtained under conditions requiring the female to transmit to the male information referring to an event observable only to her. We changed the original conditions by requiring the animals to transfer the information in the reverse direction, i. e., requiring the male to transmit rather than receive the critical information. The animals' ready success in accommodating these changed requirements, if obtained, would strongly suggest that the nature of these animals' system of acoustical communication afforded all of them the capacity to transmit information of the sort required here. If, on the other hand, the former success was instead due to the animals' ability to acquire, with time, means of meeting the demands of this particular situation, then the changed situation would require the development of new modes of action from each animal, and the course of this new learning would be available to investigation.

These changes in requirements were imposed by first demanding the animals to change the order of their paddle responses—female then male—while the S^D signals were presented to both. Then as in the original training program the male's S^D light and his Time In light were gradually moved to the female's side and eliminated, and then the remaining light assemblage was gradually moved back to the male's side. Finally, the visual barrier was drawn between the two enclosures. The work to date has progressed to the point where only 2 feet of visual access remains and consistently high performance levels are attained. However, there is some strong evidence that the female, as the visual gap has been closed to small distances, has begun to key her paddle responses to the position the male assumes in his approach to his paddles. She appears to be achieving this by either active echolocation or passive listening and our efforts presently are directed to eliminate this possibility so as to expose the animals to the requirement for social signaling.

In any case, the results of the role reversal experiment obtained so far, which show no evidence of easy interchangeability of the animals' roles in this situation, forcefully argue that the original performance success was based on very specific learning occurring during the training leading up to the actual information transfer test. Together with the results of the S^D reversal experiment, they quite clearly indicate that the natural modes of social interactions of these animals do not encompass a prior capacity for transmission of information of the kind investigated in these studies.

With this sketch the overall character of the work and its rationale we may proceed to present detailed reports of each of its phases.

PROCEDURES AND RESULTS OF INDIVIDUAL EXPERIMENTS

RETRAINING

The animals were individually reintroduced into the experimental situation, which required differential responses to steady or flashing modes of the S^D light, on two successive days at the end of July, 1966 in preparation for again requiring them to work jointly in the testing situation. It was most impressive that fourteen months after the original training terminated, the control of the animals' behavior by

the Time In light remained completely intact (the response latencies for each animal were unchanged from those of their earlier performances) and the S^D control was quickly reestablished. The female performed above the level of chance (61% correct over 108 Time In periods) while the male's performance was somewhat below chance (44% over 327 Time In periods), but improved rapidly (78% correct on the following day).

The male was subsequently worked alone for 9 sessions (with 1850 Time In periods) during which the basic experimental conditions of the 1965 tests were imposed. (During all individual training sessions the female's bridge tone was sounded manually.) The location of the male's S^D light was gradually shifted towards the female's side of the tank until it was centered between her paddles, and time restrictions were imposed which required the male to respond within 30 sec of the onset of the S^D light. Following a success level of 93% on the final session of this training stage, the male's performance dropped to 38% correct when the programmed S^D light was covered, clearly indicating his dependence upon visual cues provided by the S^D light for determination of his response.

With the S^D light centered on the female's side of the tank and the maximum duration of an S^D period ranging up to 30 sec, the animals were first required to jointly coordinate their actions on August 16, 1966. Their joint level of success ranged from 85%, during the initial session, to 98% over 588 Time In periods. During this training stage the female's paddles had been moved from the wide (0.91 m) to the close (<15.2 cm) position with no effect upon the male's performance.

During the next 9 training sessions involving 1458 Time In periods the canvas curtain, which provided a visual barrier between the two sides of the tank, was drawn gradually across the tank until no visual access remained. The animals maintained at least a 90% level of performance until the visual access was restricted to 4 feet. At this point each further restriction of access resulted in an initial decrease in successful performance before a 90% level of performance was again attained. During the final session of this training stage the animals' performance was 93% successful over 198 Times In periods.

Installation of the neoprene covered plywood acoustic barrier was the final stage in approximating the experimental conditions of the 1965 testing. Following an initial drop in performance (71% correct over 82 Time In periods) the animals' performance improved over a four day period (with 583 Time In periods) until they exceeded the

required 90% level of success. To insure stability in the animals' performance 23 training sessions (3381 Times In periods) were conducted over a six week period during which an average performance level of 94% was attained.

The remaining training sessions involved implementation of various control procedures to insure that the female was dependent upon visual signals from the S^D light and that the male was dependent upon the phonatory emissions of the female. Thus, the following conditions were individually introduced into the testing situation: (1) the acoustic door under the feeder platform was closed; (2) the programmed S^D light was covered; (3) the Time In light was covered; (4) the female's paddle array was removed and her bridge tone sounded manually; (5) cylindrical ducts, 90 cm long, were extended from the female's S^D and Time In lights; and (6) the female was restricted from entering the area within 10 feet of the lights by a net drawn across the tank. Masking of the S^D light influenced the level of performance significantly as is indicated by only a 50% success level. Performance on all other sessions remained above 90% (averaged 98%).

Table 1 summarizes the occurrence of phonatory emissions by the female and the attained performance level of the animals during the retraining period. The periods represent samples from recordings of:

TABLE 1. Performance and Female's Phonatory Productions
During Retraining

Period	S ^D Condition	Total S ^D Periods	% S ^D Periods Female		% Correct	
			Pulses	Whistles	Male	Total
A*	Steady	13	100	0	85	74
	Flashing	21	100	0	67	
B	Steady	73	93	41	88	93
	Flashing	67	69	34	98	
C	Steady	93	100	63	80	81
	Flashing	91	9	65	82	
D	Steady	279	95	33	93	94
	Flashing	344	26	33	95	
E	Steady	149	99	11	96	97
	Flashing	160	8	13	98	
B-E	Steady	594	97	33	91	93
	Flashing	662	24	33	96	

*Female only.

(A) the female working alone immediately prior to their joint efforts; (B) training sessions during which the visual barrier was complete; (C) training sessions following installation of the acoustic barrier; (D) sessions run to insure stabilization of the animals' performance; and (E) sessions during which implementation of the various control procedures was carried out.

As a final note to this summary of performance results, Table 2 presents the average time elapsing between the onset of an S^D period and the male's paddle press. The difference between his response time in pressing his left and right paddles, 3.31 and 3.38 respectively, was not statistically reliable ($t = 1.02$, $p > .10$). His average response time was somewhat longer when he pressed the incorrect paddle (3.93) than when he responded correctly (3.30). The differences between these response latencies was statistically reliable ($t = 3.64$, $p < .01$). As was found in the 1965 tests, the male's response latency is increased when the acoustic barrier is present (Period C).

TABLE 2. Mean Male Response Latencies (sec)
During Retraining

Period	Response				Total
	Paddle		Success		
	Left	Right	Correct	Error	
B	3.54	3.44	3.49	3.55	3.50
C	3.71	3.75	3.56	4.47	3.73
D	3.29	3.43	3.32	3.86	3.35
E	3.02	3.02	3.03	2.67	3.02
B - E	3.31	3.38	3.30	3.93	3.35

Throughout the retraining period sample recordings of the female's phonations during Time In periods were made. The majority of recordings were made through a single hydrophone located near the female's paddle array. Oscillographs of the obtained recordings were made to provide visual records of the acoustical events within each S^D period. These oscillographs, in conjunction with the tape recordings, permitted the reconstruction and analysis of events occurring within the critical segment of Time In periods. However, as the purpose of the work undertaken in 1966 was to reestablish the previous experimental situation (1965) and to allow the animals' behavior to stabilize

in preparation for the following stage of the experiment, the characteristics of the female's phonations will be discussed only briefly.

Results of the 1965 tests indicated that the female's production of whistles had no differential relationship to the S^D condition or the male's paddle response. We have therefore only noted the occurrence of whistles during Time In periods. Table 3 clearly indicates the lack of relationship between the occurrence of female whistle productions, the S^D condition, and the male's performance success. The probability that the female whistled on the condition that the S^D light was steady (33%) is equal to the corresponding probability for a flashing light. And, the probability that the male responded correctly on the condition that the female whistled (93%) is equal to the corresponding probability for those S^D periods during which the female did not whistle. The relative frequency of whistles is greatest during Period C, the training sessions following installation of the acoustical barrier. If the female did whistle during an S^D period she generally produced only one ($N = 295$, 71%). The occurrence of as many as four separate whistles within an S^D period was noted, however.

TABLE 3. Contingency Analysis of S^D Condition,
Male's Performance, and Female's Whistle Productions
During Retraining

	S^D Condition		Male's Response		Total
	Steady	Flashing	Correct	Error	
Female:					
Whistled	198	218	388	28	416
Did not whistle	396	444	778	62	840
Total	594	662	1166	90	1256

The 1965 data suggested a possible link between the female's whistles and the onset of S^D periods, by which the female's whistles might have served to mark this critical event for the male and thus served to synchronize the actions of the two animals. Support of this hypothesis can be found in the following results: (1) the female emitted no whistles when working alone (Period A) and (2) of the 416 S^D periods during which the female did whistle 289 (69%) of the whistle onsets were within 0.5 sec of the onset of the S^D light.

A sample recording made prior to the joint work of the animals (Period A) indicated that the female was emitting pulse trains in every

Time In period, as she was doing during the 1965 testing period. However, one of the most striking outcomes of the retraining process, which can be seen by referring again to Table 1, was the progressive reduction in the female's production of pulse signals in the flashing S^D condition. Though she continued emitting pulse trains in virtually all steady S^D periods, by the end of this retraining phase she was emitting these signals only occasionally in flashing S^D periods.

Table 4 summarizes the occurrence of her pulse trains over all runs (Periods B - E). The female emitted at least one pulse train in 730 of the 1256 Time In periods (58%). Of these 730 periods containing her pulse trains, 575 (79%) occurred when the S^D light was in steady mode and 155 (21%) occurred in conjunction with a flashing light. When the female did emit a pulse train the male pressed his right paddle in 537 instances (74%), his left paddle in 193 cases (26%). In those Time In periods that the female emitted no pulse trains (526 or 42% of total), 19 (4%) were in conjunction with a steady light, while 507 (96%) were associated with a flashing light. The male's paddle response in these instances was occasionally to the right ($N = 41$, 8%), but predominantly to the left ($N = 485$, 92%). Over all sessions the male was somewhat more likely to respond correctly if the female did not emit a pulse train (95%) than if she did pulse (91%).

TABLE 4. Contingency Analysis of S^D Condition, Male's Performance and Female's Pulse Train Productions During Retraining

	S ^D Condition		Male's Response				Total
			Paddle		Success		
	Steady	Flashing	Right	Left	Correct	Error	
Female:							
Pulsed	575	155	537	193	666	64	730
Did not pulse	19	507	41	485	500	26	526
Total	594	662	578	678	1166	90	1256

In most of the S^D periods characterized by the presence of pulse trains (730), the female produced only one ($N = 671$, 92%). Multiple pulse trains, normally two but as many as four separate trains (counted as such when separated by more than 0.5 seconds), occurred in 8% ($N = 59$) of the S^D periods. There was no reliable difference in the occurrence of multiple pulse trains for the two S^D light conditions

(51% in steady, 49% in flashing). The success of the male's response was not adversely affected by the presence of more than one pulse train (86% correct, 14% error). In those S^D periods that the female produced more than one pulse train the first pulse train has been considered in the analyses that follow.

The previously reported work had indicated the potential importance of three parameters of the pulse trains emitted by the female. The overall averages of measurements of these parameters of the pulse trains are presented in Table 5 with respect to the mode of the S^D light, steady or flashing, and the male's paddle response, right or left.

TABLE 5. Analysis of Onset Times, Durations, and Repetition Rates of Initial Female Pulse Trains With Respect to S^D Light Condition and Male's Paddle Response During Retraining

	Onset		Duration		Repetition Rate		N
	Mn.	S. D.	Mn.	S. D.	Mn.	S. D.	
Period A							
Steady	0.58	0.50	3.22	1.03	74.8	14.5	13
Flashing	1.25	0.72*	0.74	0.39*	54.8	14.6*	21
Period B							
Steady	0.80	0.45	2.19	0.88	32.8	15.2	68
Flashing	1.14	0.65*	0.66	0.45*	31.3	15.3	46
Right	0.77	0.44	2.23	0.88	32.4	15.0	60
Left	1.12	0.62*	0.84	0.68*	31.9	15.5	54
Period C							
Steady	1.10	0.59	1.53	0.61	37.2	14.2	93
Flashing	1.37	0.63	0.63	0.54*	40.4*	25.2	8
Right	1.08	0.58	1.54	0.64	37.2	15.6	77
Left	1.23	0.64	1.18	0.61**	38.2	14.7	24
Period D							
Steady	1.37	0.61	1.71	0.76	27.1	11.7	226
Flashing	1.43	1.05	0.55	0.42*	37.1	27.4*	88
Right	1.36	0.64	1.67	0.77	27.3	12.3	256
Left	1.46	0.96	0.79	0.74*	35.5	25.8*	98
Period E							
Steady	1.00	0.53	1.96	0.83	18.7	6.7	148
Flashing	1.98	1.37**	0.23	0.14*	40.0	23.0***	13
Right	0.99	0.53	1.96	0.82	18.6	6.3	144
Left	1.80	1.26**	0.67	0.95*	36.0	23.1*	17

Level of significance of "t" scores between pairs of adjacent means: p < 0.01; p < 0.02**; p < 0.05***.

All temporal measurements of events occurring within an S^D period were based upon a zero point of 5.0 seconds after the onset of the Time In light. In contrast to the 1965 material, there was no problem in demarcating the onset of S^D periods for the relay switch controlling the onset of the S^D light was registered as a transient click on the recordings of the experimenter's voice channel. The onsets of pulse trains were determined simply by measuring the time interval between the onset of the S^D period and the occurrence of the first pulse of a train. The duration of a pulse train was determined by the time interval between the first and last pulse of a train. The average repetition rate (pulses per second) of a pulse train was obtained by dividing the total number of pulses by the duration of the train.

It is apparent from Table 5 that the pulse trains the female emits when the S^D mode is steady and those to which the male responds by pressing his right paddle are generally characterized by earlier onsets and longer durations than pulse trains associated with the flashing light and the male's left paddle presses. The differences between the onset times for both the light condition and the male's response were statistically distinct during Periods A, B ($p < 0.01$), and E ($p < 0.02$). The corresponding differences in the duration of the pulse trains also obtained statistical significance ($p < 0.01$) in all periods (A - E), with the exception of Period C, right versus left (where $p < 0.02$). The characteristic association of these two parameters with S^D light conditions and the male's paddle response is comparable to that found in 1965. During the 1965 experiment the repetition rate of pulse trains associated with a steady light was somewhat higher than it was for those pulse trains associated with a flashing light (26.7 and 22.2 respectively; statistically reliable at 0.05 confidence level). During the period of the present investigation it is interesting to note the clear shifts in the associations between the repetition rates, S^D conditions, and the male's responses. During Period A, when the female was working alone, the repetition rates were quite high, following the 1965 pattern of association, and were distinct at the 0.01 confidence level. When the animals were working together, during Periods B and C, the repetition rates are much lower and cannot be considered statistically distinct in regard to either the light mode or the male's response ($p > .50$ for all comparisons). In the two final periods, D and E, the female is pulsing in only 20% (101/504) of the flashing S^D periods. However, at this time those pulse trains associated with a steady light have lower repetition rates than do those that occur in conjunction with a flashing light. The correlation of repetition rate and the male's paddle response follows accordingly, i. e., "fast" and "slow" repetition rates are associated with left and right paddle presses, respectively. All comparisons are significant at the 0.05 confidence level or beyond.

PLAYBACK EXPERIMENT I

The results just reported, together with those obtained in 1965, permitted the formation of a fairly clear characterization of the nature of the information transmission process. The strongest conceivable test of these inferences concerning the critical features of the animal's pulse trains in determining the male's actions would be to replace the female's actual presence with selective acoustical recordings of her prior emissions. To this end a playback experiment was devised which, if successful, would permit systematic manipulation of the temporal and frequency characteristics of the original signals. The male's response to these experimental signals would then provide information concerning the critical features involved in the information transmission.

The recordings that were to provide the stimulus materials for this initial playback experiment were obtained during several sessions of retaining Period E, in which the various control procedures were implemented, together with video tape recordings of the animals' movements as viewed from cameras situated on a catwalk above the tank. The animals' sound emissions were recorded at 60 ips on a multi-channel instrumentation recorder which, with the associated components, provided a record-reproduce system with essentially flat frequency-response characteristics to beyond 100 kHz. The female's signals from two of the above sessions were chosen, on the basis of the quality of the audio and video recordings, as the stimulus materials to be used in the playback stage of the experiment. The first of these sessions was run with the acoustical barrier complete. By monitoring the audio track of the video recordings during this session it was possible to determine the female's location in the tank at the onset of her signaling. The second session was run with the female confined by a net drawn across the tank 10 feet away from her light and paddle arrays. During this session the female's hydrophone was attached to the net which confined her in order to reduce the effects of her changing position upon the recorded signals.

To see if the male could still respond appropriately to the earlier signals two sessions of the 1965 tests were also selected. During the first of these (Run IX) the acoustical barrier extended across approximately two-thirds of the tank; the acoustic barrier was complete, although a gap had been made beneath the feeders, in the second session (Run XIV). It will be remembered that the characteristics of the female's pulse trains, including the absence of pulse trains, had changed during the period under consideration (1965 versus 1966).

One hundred and nineteen S^D periods (64 steady, 55 flashing) were chosen from the above sessions to be used in the playback experiment. These S^D periods were selected because (1) they contained no whistles from either animal nor pulse trains of the male and (2) the male had responded correctly. Each of the original recordings from each session was then edited to leave only those S^D periods selected for the playback experiment. The characteristics of the female's pulse train emissions in the selected S^D periods are presented in Table 6; she emitted no pulses in 31 of the selected flashing S^D periods.

TABLE 6. Characteristics of Pulse Trains Selected for Stimuli in Playback I

	Onset		Duration		Repetition Rate		N
	Mn.	S.D.	Mn.	S.D.	Mn.	S.D.	
Playback 1 (Run IX)							
Steady	1.13	0.17	1.60	0.32	20.0	2.8	9
Flashing	1.38	0.40	1.21	0.37	17.5	2.3	14
Playback 2 (Run XIV)							
Steady	1.58	0.16	2.39	0.53	22.9	5.4	12
Flashing	2.83	0.81	1.32	0.80	19.4	8.6	7
Playback 3 (7 Nov 66)							
Steady	0.59	0.20	1.56	0.52	23.9	5.4	23
Flashing	1.39	0.49	0.16	0.07	42.8	1.3	3
Playback 4 (12 Dec 66)							
Steady	1.56	0.66	2.82	1.00	12.8	2.0	20
Flashing

Strips of sensing tape were then applied to the magnetic tape at four critical temporal locations within each Time In period so that a photocell sensor could be used together with a stepping relay to govern the following events:

- (1) The Time In light onset (5 sec before the S^D light onset of the original recording).
- (2) The onset of reproduce amplification, allowing reproduction of the recordings of the female's channel to enter the tank.

- (3) The offset of reproduce amplification (just prior to onset of the male's echo ranging pulses, which he characteristically emitted just before hitting his paddles).
- (4) Stopping the tape deck, so that each Time Out period in the playback experiment could be manually controlled.

The signals recorded on the female's channel were delivered to a high frequency power amplifier whose output drove a single element transducer located in the water at about the same position as the female when she began emissions of her pulse trains during the original recordings. The amplitude of the reproduced signals was adjusted to approximate the level on the original recording.

Considerable difficulties were faced in working out the final arrangements for delivering the reproduced signal to the male at their original temporal locations in the Time In periods. While these technical kinks were being smoothed out (which required about a month in late January and early February) the animals were worked together on eight occasions to keep the male's performance at high levels before the playback tests commenced.

Tests of the playback experiment with the male began early in February, 1967. Over a two month period 32 sessions (involving 2781 Time In periods) were conducted during which an overall performance level of 70% was attained.

The playback programs derived from November and December, 1966 were run initially (for 68 Time In periods) and the male's performance fell below the level of chance (48% correct). Therefore, tape loops were devised whereby for each loop only one signal associated with steady and one silent period associated with flashing would be delivered into the tank. The male was worked with the tape loop signals for four sessions (involving 229 Time In periods) and attained a success level of 87% during the final session. Work was then resumed with the complete playback programs. Over approximately 500 Time In periods, during which the reproduce amplifier gain was gradually increased, the male's overall level of performance was 65%. During this period he made a disproportionate number of right paddle presses (72% of his total responses) when compared with the number of "steady" stimuli that were presented to him (59% of the total stimuli). On the assumption

that he was reacting to tape hiss when no pulse train ("flashing" signal) was presented, and therefore pressing the right paddle, the reproduce gain for the "flashing" signals was differentially reduced. More than 600 Time In periods were run in which the amplification of "steady" stimuli was greater than that of "flashing" stimuli. The male's performance under these conditions reached a 76% success level and the disproportionate number of right paddle presses was eliminated. Then, the difference in amplification gains for the two types was gradually equalized over 240 Time In periods, with no adverse effects upon the male's performance (86% correct) and the distribution of his paddle presses was proportionate to the distribution of stimuli presented.

However, when the gain levels were again equalized in a final series of almost 1000 Time In periods, the male's level of success, although intermittently quite high (up to 98% in 46 consecutive Time In periods), was nonetheless far from perfect overall (66% success for the final series). During the course of these final tests he again developed a marked position bias in favor of his left paddle (64% of his total responses), although "flashing" stimuli occurred in only 53% of the Time In periods.

Thus there was little in the results of this extensive testing to suggest that the reproduction of the recordings of the female's signals were effective in governing the male's paddle-pressing actions. Though he often attained levels of performance success that were consistently above chance, these departures can be as much ascribed to learning that took place during the prolonged testing as to the generalizable effectiveness of the recordings of the female's originally effective signals.

These negative results were naturally quite discouraging. However, there was abundant reason to suppose that they arose not from the strategy of the playback experiment, but from unresolved problems inherent in the actual procedures used to conduct it. (At no time did the male refuse to work and his response latencies, regardless of his success, occurred within the appropriate time limits.) The problems, of course, centered around the reliable delivery of a good reproduction of the original signals at the appropriate times. Many difficulties were confronted in tripping the stepping relay, which governed the program of events within the experimental chamber as well as the reproduce amplifier. But even when this was corrected the recordings made during the playback experiment showed that very prominent switching transients resulted at each relay step and entered the water through the input hydrophone. And, though the original

recordings had been essentially flat from 2 to beyond 100 kHz, the hydrophone used as the input transducer introduced very severe distortion. This, together with the switching transients, produced sufficient degradation in the quality of reproductions of the original signals to plentifully account for the male's lack of performance success and the failure of the experiment. While it was not financially possible to replace the switching functions with solid state circuits, and thus eliminate the switching transients, the possibility of developing a better input transducer did exist.

It was, therefore, decided to work with the animals on the next set of questions, concerned with the effect of reversing the significance of the S^D signals while a new input transduce system was developed. Since we had considerable confidence that the animals could successfully accommodate this reversal of S^D relationships, our plan was to follow this S^D reversal training with another playback experiment in which the better input transducer system could be used.

S^D REVERSAL TRAINING

Each animal was worked individually under the original S^D conditions prior to beginning their S^D reversal training. Although they had worked (together) only eight times in 1967 (from January 3 to February 8) each animal attained a performance level of 100% (the male over 16 Time In periods, the female over 25). Recordings made of the female's phonations during review of the original S^D conditions indicated that her signaling in relation to S^D mode was similar to that found prior to the playback experiment, i. e., she continued to emit pulse trains in all steady S^D periods and emitted no signals in the flashing S^D periods.

Immediately following the review of the original task, the S^D reversal training was begun, with each animal continuing to be worked alone. Bridge signals usually associated with the other member of the pair's paddle presses were provided by the trainer.

The male's S^D reversal training began on April 4 with the S^D light centered on his side of the tank. He reached the 90% success criterion with the new conditions in three days of training (436 Time In periods). Then the position of the S^D light was gradually shifted until it occupied the appropriate position on the female's side. The female's S^D reversal training began on April 28 and continued throughout the month of May. Eighteen sessions, with 911 Time In periods, were run before her level of performance exceeded 90%.

The remaining portion of the training period for each animal involved gradually moving the S^D light from its original location to a central position between the paddles on the opposite side of the tank. The male required 13 sessions, with 1582 Time In periods, to complete this final preparation. The female required 8 sessions, with 222 Time In periods, to complete her training. The extent of the shifts in light location was governed by requiring a 90% performance level for each animal over successive samples of 50 Time In periods.

Although the female had previously not been emitting signals in the flashing light condition, by the fourth day of the S^D reversal training she emitted pulse trains in all Time In sessions, steady and flashing, and continued to do so through the next four month period (May-August). However, detailed analyses of the female's signals was not performed for sessions recorded prior to August 22, 1967.

June 1, 1967 was the first time that the animals were required to work together again. In the first training stage the location of the male's S^D light was again gradually shifted from its original position towards the female's S^D light until it was close enough to be removed. This required eight days and 920 trials to accomplish.

The next training stage involved restricting the visual access between the two animals by gradually drawing a canvas curtain across the center of the tank. Following an initial decrease in performance a 90% level of success was maintained until the visual access was restricted to 4 1/2 feet. As the visual restriction became complete performance gradually declined from 95% (access 4 1/2 feet) to 69% (no visual access). The limitation of visual access took place over a three day period and involved over 360 trials.

Although the usual requirements of a 90% success level had not been met, the acoustic barrier (which is also a visual barrier) was installed and the door between the feeders was left open. With no visual or acoustic access between the animals 653 trials were run (over a period of 5 days) during which the male's success level ranged from 45% to 54%.

During the following 19 days of training (2804 trials) a 3.1 m section of the acoustic barrier was removed between the light and paddle configurations of each side; the canvas curtain was also withdrawn by the same amount. Then the curtain was gradually redrawn to restrict this visual access to 12 inches. During this "remedial" training the extent of the visual access was controlled so as to maintain a 90% level of success.

The final stages of the experiment, from August 22 to October 9, will be reported in detail. These trials, in which acoustical recordings were made and the phonatory emissions of the female analyzed, have been divided into five periods based upon the tank conditions and the male's level of performance success.

Period I, (August 22 - 25): In this group of runs the acoustic access between the two animals remained at 4 feet; the visual access ranged from 12 to 6 inches. The male maintained a performance level of at least 80%. During these and all preceding trials, when the S^D light was in flashing mode a tone burst occurred at the onset of the light. This tone burst, designed to mark the onset of flashing S^D periods on the voice channel of the recordings, was generated in the control booth adjacent to the tank. The sound, while not entering the water, was discriminable to human hearing in the experimental area. It began to be suspected that the male was keying his response to this airborne sound when it was noticed that he was approaching his paddles with his head out of the water. To check this possibility the animals were worked for two days alternately with and without the tone bursts associated with a flashing light. The male achieved a success level of 86% in the 111 trials in which the tone bursts were present, but his performance dropped to 66% on those 230 trials run with no tone bursts. Because of this evidence that the male's responses were at least partly governed by these tone bursts, they were eliminated in subsequent trials. Those trials with tone bursts define the extent of Period I when the animals were not exposed, at least completely, to the critical conditions because of the male's sensitivity to this accidental condition.

Period II, (August 25 - 31): In this period the removal of the tone burst associated with the flashing S^D condition re-exposed the animals to the full requirements of the test with the acoustic and visual access between the two animals held constant at 4 1/2 feet. The male's performance on these runs ranged from 54% to 74% on the final day.

Period III, (September 5 - 11): By September 5 the male's performance had increased to the level attained before the flashing tone bursts were eliminated. During the latter part of this group of trials the visual barrier was completed with only a 2% drop in performance level from the preceding (unrecorded) run. The virtual constancy of performance at this stage was not unexpected, for observation of the approach pattern of the male gave no indication that he was utilizing his visual access to the S^D light in determining his paddle response when this access was reduced to a 6 inch gap in the barrier. The performance level of the male ranged from 80% initially to 100% on the final

day of this group of runs. Eleven trials (which are not incorporated in the following analyses) were run during this period in which the female's S^D light and paddles were removed from the tank, but the Time In indicator light remained. Although the male responded within the allotted time, his performance level fell to 45% indicating his dependence upon the S^D information presented to the female.

Period IV, (September 14 - 18): In this group of runs the acoustic barrier was completed, although the door at the far end of the tank under the feeders remained open. On the first trials run with the acoustic barrier in place the male's performance dropped 6% below that of the previous run (both unrecorded) to 88%. On the first recorded group of trials the male's performance inexplicably dropped to 74% then climbed to 100% on the remaining two recorded runs. During the two latter runs the female's paddles were, for the first time, moved to their close position (15.2 cm as opposed to .91 meter). The position change of the paddles had no adverse effect upon the male's performance.

Period V, (October 5 - 9): In the four recorded runs of October both the visual and acoustic barriers were complete; the door in the acoustic barrier was closed throughout. Manipulation of the female's paddle array occurred in four stages: (1) paddles in wide position, (2) paddles in close position, (3) female's paddles removed from tank, and (4) female confined to far end of tank by a net barrier across her side of the tank. The male's performance dropped from 100% during (3) to 91% during (4) but the relationship between his performance and her confinement is not clear.

An overall examination of Table 7 indicates that the only experimental conditions which markedly impaired performance were eliminating the trainer's tone bursts in the control room (Period II, August 25 - 31) and removal of the female's S^D light (September 11).

Various control procedures effectively eliminated the possibility that the male had been responding to adventitious acoustical cues from the programming and recording equipment or the possibility that the male had been basing his response upon the female's position in her approach to the paddles. Observations of both the male's and female's patterns of approaches to their paddles were made utilizing video tape recordings of the October runs (Period V). Although the male was visible in only a few trials two approach patterns were noted (the same as 1965). His most frequent pattern was to approach the left paddle straight on then swerve obliquely about 4 feet in front of the paddles when going on to hit the right paddle. A second approach pattern was

TABLE 7. Performance and Female's Phonatory Productions During S^D Reversal

Period	Date	S ^D Condition	Total	% S ^D Periods	% Correct	
			S ^D Periods	Female Pulses	Male	Total
I	22 Aug.	Steady	12	100	83	87
		Flashing	22	100	96	
	23 Aug.	Steady	18	100	83	81
		Flashing	19	100	79	
	25 Aug. , No. 1	Steady	14	100	93	95
		Flashing	7	100	100	
II	25 Aug. , No. 2	Steady	10	100	70	68
		Flashing	15	100	67	
	28 Aug.	Steady	7	100	86	67
		Flashing	8	100	50	
	30 Aug.	Steady	29	100	52	54
		Flashing	7	100	100	
	31 Aug.	Steady	17	100	71	74
		Flashing	10	100	80	
III	5 Sept.	Steady	28	93	82	80
		Flashing	23	91	96	
	6 Sept.	Steady	11	100	91	91
		Flashing	11	55	91	
	8 Sept. , No. 1	Steady	15	100	87	91
		Flashing	7	100	100	
	8 Sept. , No. 2	Steady	13	100	77	87
		Flashing	10	70	100	
	11 Sept. , No. 1	Steady	6	33	50	45
		Flashing	5	20	60	
	11 Sept. , No. 2	Steady	3	100	100	100
		Flashing	2	100	100	
IV	14 Sept.	Steady	11	100	73	74
		Flashing	16	69	75	
	15 Sept.	Steady	10	100	100	100
		Flashing	10	10	100	
	18 Sept.	Steady	11	100	100	100
		Flashing	9	22	100	
V	5 Oct. , No. 2	Steady	18	100	100	100
		Flashing	12	0	100	
	5 Oct. , No. 3	Steady	16	100	94	97
		Flashing	15	7	100	
	9 Oct. , No. 4	Steady	16	100	100	100
		Flashing	14	21	100	
	9 Oct. , No. 5	Steady	18	100	94	91
		Flashing	16	6	88	

noted during which the male swam next to the center barrier approximately halfway down the tank then proceeded to the paddles.

Table 8 presents the average time elapsing between the onset of the S^D period (5 seconds after Time In onset) and the male's paddle press. As was indicated in 1965 and 1966, it appears that his response latencies were primarily influenced by the extent of the acoustic barrier between the two animals. There was a slight difference in his overall

TABLE 8. Mean Male Response Latencies (sec)
During S^D Reversal

	Response				Total
	Paddle		Success		
	Left	Right	Correct	Error	
<hr/>					
Period I					
22 Aug.	3.62	3.48	3.50	3.82	3.52
23 Aug.	4.04	3.68	3.75	4.35	3.86
25 Aug. No. 1	3.94	3.64	3.84	3.55	3.83
Period II					
25 Aug. No. 2	4.15	3.58	3.81	3.95	3.86
28 Aug.	3.98	3.77	3.78	4.18	3.91
30 Aug.	4.47	4.95	4.65	4.91	4.75
31 Aug.	3.82	3.97	3.86	3.99	3.89
Period III					
5 Sept.	3.40	3.06	3.32	2.48	3.22
6 Sept.	3.29	3.02	3.12	3.52	3.16
8 Sept. No. 1	3.33	2.58	3.08	2.46	3.02
8 Sept. No. 2	3.29	3.17	3.26	2.96	3.22
11 Sept. No. 1	5.40	5.18	5.19	5.40	5.30
11 Sept. No. 2	4.03	4.24	4.11	...	4.11
Period IV					
14 Sept.	4.30	4.00	4.04	4.37	4.13
15 Sept.	3.96	3.97	3.96	...	3.96
18 Sept.	4.24	4.18	4.21	...	4.21
Period V					
5 Oct. No. 2	4.48	4.02	4.29	...	4.29
5 Oct. No. 3	4.35	4.13	4.31	2.10	4.24
9 Oct. No. 4	4.93	4.73	4.84	...	4.84
9 Oct. No. 5	5.69	5.33	5.55	5.25	5.53
Total	4.15	3.90	4.01	4.15	4.03

response times in pressing his left and right paddles, 4.15 and 3.90 seconds respectively, which was statistically reliable ($t = 2.92$ with 514 degrees of freedom, $p < .01$), although this apparently was due to approach differences. No reliable differences were found between his response times with respect to correct versus error responses.

The female's approaches were recorded during the latter two runs in October when her paddle array had been removed. Even so, her approach patterns were observed to be quite distinct depending upon the mode of the S^D light. During the first run when the paddles had been removed but the female had access to the entire tank she consistently swam directly in line with the light when it was in a flashing mode (in 3 instances she then oriented herself toward the center barrier). When confined in the following run she again oriented herself directly towards the light when it was in flashing mode. During the first of the video recorded runs when the S^D signal was in the steady mode she swam alongside the barrier in 11 instances and turned partially toward it in 5 instances before swinging back towards the light. In the following run, during which she was confined, she in every instance oriented herself directly (13) or partially (5) towards the junction of the barrier and the net which confined her. The departure from a straight-on orientation to the light in the direction of the barrier in these instances is of great interest because it was in these S^D conditions that she was emitting signals.

Turning now to the nature of the signals the female produced in this S^D reversal experiment, reexamination of Table 7 shows a gradual evolution in her signaling that closely parallels the shift which occurred during the retraining work. Throughout all trials (194) of Period I and II the female emitted at least one pulse train in each S^D period, steady and flashing. The decrease in occurrences of pulse trains associated with a flashing S^D light took place slowly. The percent of flashing S^D periods during which the female emitted a pulse train decreased from 80% in Period III to 40% in Period IV to 9% in Period V. As is indicated in Table 9 the change in the female's signaling pattern had no adverse effect on the male's level of performance (98% correct when the female emitted no pulse trains).

In most of the S^D periods in which the female did emit pulse trains, she produced only one (88%). Multiple trains, normally two but as many as three separate trains (counted as such when separated by more than 0.5 seconds), occurred in 12% of the S^D periods. Multiple trains were more likely to occur in steady S^D mode (82%) than in flashing S^D mode (18%); the male was more likely to respond correctly (86%) than

TABLE 9. Contingency Analysis of S^D Condition, Male's Performance, and Female's Pulse Train Productions During S^D Reversal

	SD Condition		Male's Response				Total
			Paddle		Success		
	Flashing	Steady					
			Left	Right	Correct	Error	
Female:							
Pulsed	148	272	251	169	353	67	420
Did not pulse	83	2	2	83	83	2	85
Total	231	274	253	252	436	69	505

incorrectly (14%). The majority of these multiple pulse trains occurred in the runs from 14 September to 9 October. To some extent the preponderance of multiple pulse trains in these runs was probably associated with the longer durations of the S^D periods due to longer male response times. The latter member of these multiple trains characteristically occurred within one second of the male's response (41 to 91% began within 1.0 sec, the remaining 4 or 9% began within 1.2 sec), and these 45 trains are not considered in the present analysis.

In those S^D periods in which the female produced more than one pulse train the first pulse train was considered in the analyses (N = 45), except for 6 (all within Period II) in which the final pulse train was considered. These were treated as exceptions because the first pulse trains in these S^D periods appeared to be "false starts"; they were characterized by early onsets (<1.00 sec), short durations (5/6 <1.00 sec), and were followed by a second pulse train which was continuous from its onset to the male's paddle press.

The same 3 parameters of the female's pulse trains as had been considered in the earlier work were analyzed in her emissions during the S^D reversal experiment presented by periods in Table 10 with respect to S^D light condition and the male's response.

The onsets of the pulse trains were determined simply by establishing the period of time which elapsed between the onset of the S^D period and the occurrence of the first pulse of a train. The duration of a pulse train was determined by the time interval between the first and last pulse of a train (N = 85) or more frequently (N = 335) by the time interval between the first pulse and the male's paddle press, for the pulse trains usually (80%) continued beyond the male's response. The

TABLE 10. Analysis of Onset Times, Durations, and Repetition Rates of Pulse Trains With Respect to S^D Light Condition and Male's Paddle Response During S^D Reversal Training

	Onset		Duration		Repetition Rate		N
	Mn.	S.D.	Mn.	S.D.	Mn.	S.D.	
Period I							
Steady	0.85	0.56	2.66	0.80	34.0	16.2	44
Flashing	1.97	0.50*	1.67	0.92*	15.8	5.8*	48
Left	1.00	0.67	2.66	0.81	34.1	16.0	43
Right	1.82	0.65*	1.69	0.93*	16.1	6.8*	49
Period II							
Steady	1.25	0.66	2.82	1.28	26.7	17.1	62
Flashing	2.31	0.63*	1.94	1.08*	18.6	8.8*	40
Left	1.36	0.72	2.75	0.91	29.3	14.4	50
Right	1.96	0.83*	2.20	1.51***	18.0	13.4*	52
Period III							
Steady	0.88	0.57	2.31	0.72	22.8	9.0	66
Flashing	2.04	0.77*	0.94	0.50*	13.7	5.8*	41
Left	1.04	0.26	2.40	0.69	23.5	8.8	58
Right	1.83	0.86*	1.06	0.58*	14.4	6.5*	49
Period IV							
Steady	0.92	0.49	2.90	0.75	29.6	14.6	32
Flashing	2.58	0.81*	1.13	0.63*	12.0	7.6*	14
Left	1.03	0.62	2.74	0.77	26.3	15.0	33
Right	2.43	0.99*	1.42	1.18*	19.1	14.5	13
Period V							
Steady	1.32	0.80	2.76	1.10	27.2	7.4	68
Flashing	2.45	0.78*	1.11	0.32*	12.0	11.0*	5
Left	1.29	0.71	2.76	1.12	27.2	7.2	67
Right	2.50	1.32***	1.36	0.21*	13.7	12.3**	6

*Level of significance of "t" scores between adjacent means:
 $p < 0.01^*$; $p < 0.02^{**}$; $p < 0.05^{***}$.

pulse repetition rate in the pulse trains occurring in steady S^D periods were characteristically slow at the start followed by a marked increase, whereas the trains emitted in the flashing S^D periods did not usually depart from this slow initial repetition rate. This difference is most apparent immediately prior to the male's response. However, study of his approach pattern (both in October 1967 and November 1966) had shown him never to change his course towards a given paddle in the final one second preceding his paddle response. That is, his decision point occurred earlier than one second before his actual response. We

have therefore established the 1/2 second period immediately prior to this (1.50 to 1.00 seconds before his paddle press) as the last interval during which the repetition rate of the female's pulse trains could have influenced his response. Whenever possible, the repetition rate was measured in this interval. However, if a pulse train did not continue through the final second prior to the male's response or began less than 1.50 seconds before his response, the repetition rate was measured, respectively, during the final or initial 0.50 sec of the pulse train. In those instances where the duration of the pulse train was less than 0.50 sec the total duration was used to calculate the repetition rate.

As can be seen by referring again to Table 10 the pulse trains the female emitted when the S^D mode was steady and those to which the male responded by pressing his left paddle are characterized by early onsets, long durations, and fast repetition rates. When she emitted pulse signals in the flashing S^D condition, and/or when he responded to the right paddle, the pulse trains had comparatively later onsets, shorter durations, and slower repetition rates. These parameters thus distinguish her emissions to the two S^D conditions in exactly the same manner that had obtained before the S^D reversal training, i. e., before the significance of the S^D light signals had been changed. This equivalence of signals with respect to the light conditions extends also to the female's strong tendency to eliminate emissions in the flashing S^D condition, which appeared in the late stages of training in both the relearning and S^D reversal training. It is quite clear from these results that her signals therefore referred to the condition of the S^D light rather than the paddles. If one were to try translating the semantics of these signals into English, then, one would have to say that they were comments about the state of the S^D light instead of comments about which paddle was appropriate on a given occasion, for if the signals had referred to the paddles then the signals would have had to be changed with the imposition of the S^D reversal conditions. The fact that the signals did not change with respect to the light conditions accords well with the possibility that the female's signal productions may have derived originally from her orientation responses to the S^D lights.

As has been noted, the transition from the female's tendency to pulse in every S^D period to her pulsing only when the S^D light was in steady mode took place gradually with no adverse effect upon the male's performance. (In fact the only time the male hit his left paddle when receiving no signal from the female occurred in Period V; the "no pulses, left hit" in Period III may confidently be excluded for he responded 0.76 seconds after the onset of the S^D period.) If, as suggested earlier, signals occurring within the final second of an S^D period have

only minimal effect upon the male's response an increase in the occurrence of these late signals in association with a flashing light would serve as a prelude to (1) the female's eventual extinction if signaling to a flashing light, (2) the association of late (or no) signals with a right paddle press for the male. The occurrence of pulse trains within one second of the male's response is almost exclusively ($N = 41/42$, 98%) restricted to flashing S^D periods, and is exclusively restricted to right paddle presses. As is indicated in Table 11 the proportion of these late (within one second of the male's response) pulse trains to a flashing light increased steadily from Period I to III and culminated in Periods IV and V with the greatest proportion of flashing S^D periods characterized by no pulse trains.

TABLE 11. Relationship of Female's Pulse Train Onset to Male's Response Latency During Flashing S^D Periods of S^D Reversal Training

	$\Delta B. R. L.$ and Pulse Train Onset >1.00	<0.99	No Pulse Train	Total S^D Periods Flashing
Period I	41 (.854)	7 (.146)	0	48
Period II	31 (.775)	9 (.225)	0	40
Period III	21 (.412)	20 (.392)	10 (.196)	51
Period IV	10 (.286)	4 (.114)	21 (.600)	35
Period V	4 (.070)	1 (.018)	52 (.912)	57

The characteristic differences of the various parameters of the pulse trains are maintained throughout the period under study but vary according to the calendrical groupings of runs, therefore analysis will be based on the periods individually.

In order to establish the degree of correlation that existed between any two of the above pulse train parameters, regardless of S^D mode or the male's response, Pearsonian correlation coefficients were calculated between each of the paired parameters for each period. Table 12 presents the obtained correlations, and shows that, with the exception of the pulse trains of Period V, the various parameters are not independent of each other. The highest correlation occurred between the onset and duration of a pulse train, while the smallest correlation is generally found between the onset and repetition rate of pulse trains.

TABLE 12. Pearson's Correlation Coefficient, r_{xy} , for Paired Parameters of Female Pulse Trains During S^D Reversal

Variables	Period					
	I	II	III	IV	V	I-IV
Onset, Duration	-.520*	-.562*	-.615*	-.746*	-.140	-.54*
Duration, Repetition Rate	.450*	.190	.431*	.359**	.119	.38*
Onset, Repetition Rate	-.359*	-.255*	-.298*	-.278	-.004	-.30*
Degrees of Freedom	90	100	105	44	71	345

* Level of significance of r_{xy} scores for paired parameters: $p < 0.01^*$; $p < 0.05^{**}$.

While it is of interest to note the extent of correlation between various parameters of the pulse trains, the critical question, of course, is the relationship that exists between these parameters and the mode of the S^D light and their relationship to the male's response. We proceeded therefore to examine the individual measurements within each parameter in relation to the S^D light mode, steady or flashing, and to the male's paddle response, left or right. These analyses will be presented now, except for Period V when the female rarely emitted pulse signals in flashing S^D periods (91%) and the male's responses were almost exclusively to his right paddle when she did not pulse (98%). First, Point-biserial correlations were calculated between each parameter (continuous variable) and the binary variables (steady versus flashing or left versus right). Table 13 presents these correlations for the various parameters in relation to both S^D light mode and the male's response. The onsets of the pulse trains generally show the highest levels of correlation with the light mode. This is not surprising, for the duration of a pulse train was usually determined by the male's response time, and the repetition rate was measured during a fixed interval prior to his response. Thus, of the parameters under consideration, only pulse train onset is independent of the timing of the male's actions. When the correlation values of Period II are compared with the other periods for each parameter they show the least correlation with S^D light mode, and it is during this period that the male's success level is lowest. This would suggest that (1) although the airborne tone bursts from the control room had undoubtedly been the major determinate of the male's actions in the previous group of runs, the female's signals were also influencing his responses, and (2) that the decreasing success of the male had an adverse effect upon the consistency of the female's signals.

TABLE 13. Point-Biserial Correlations for Each Pulse Train Parameter Partitioned According to S^D Light Mode and Male's Paddle Response During S^D Reversal

	N	Steady, Flashing	Left, Right
Onset			
Period I	92	-.7246	-.5250
Period II	102	-.6218	-.3604
Period III	107	-.6521	-.4563
Period IV	46	-.8068	-.6456
Periods I - IV	347	-.6617	-.4321
Duration			
Period I	92	.4928	.4834
Period II	102	.3338	.2162
Period III	107	.7163	.7247
Period IV	46	.7512	.5470
Periods I - IV	347	.5057	.4373
Repetition Rate			
Period I	92	.6044	.6001
Period II	102	.2652	.3749
Period III	107	.4869	.5012
Period IV	46	.5318	.2133
Periods I - IV	347	.4270	.4246

The obtained levels of correlation between pulse train parameters and the male's paddle response are generally not closely commensurate with the levels of correlation obtained between these parameters and the S^D condition. These correlations are in general concordance in Periods I and II, though considerably lower in Period II than in Period I. In these periods the repetition rate of the pulse train is most closely correlated with the male's response. The generally low correlations obtained for Period II serve to further indicate the male's previous dependence upon the airborne tones in determination of his response. During Period III, when the male's performance had recovered from the removal of the S^D tones, duration shows the highest correlation with response. In Period IV, for the first time, the paddle choice and light mode correlations are in total agreement and it is in this period that the male's performance levels are highest.

While the obtained correlations between the male's response and the parameters of the female's pulse emissions show impressive degrees of statistical relationship, the distributions of the measurements

on these parameters are far from discrete when partitioned according to the S^D light mode or the male's response. Therefore, the problem is to try to develop a statistical procedure such that the specification of one or more of the characteristics of a pulse train would permit the prediction of the level of the male's performance with some degree of accuracy.

A relatively simple and straightforward method of partitioning each of the three pulse train parameters was used to develop such a procedure. For each of the calendrical periods (I - IV) the frequency distributions for each parameter were separated with respect to the condition of the S^D light (steady or flashing). Then the median value of those measurements in the overlapping portions of the two distributions was determined. These values, presented in Table 14, were taken as decision cut-off points for the parameter in question, i. e., the decision to predict, on the basis of these measurements of the pulse train parameters, the S^D condition. On the assumption that the male would make the appropriate paddle response depending on whether a given measurement fell above or below the critical cut-off points, it was then possible to predict his performance success on the basis of these acoustical features. Similarly these measurements of individual acoustical parameters could be combined to provide joint decision procedures for predicting S^D condition and paddle choice.

TABLE 14. Decision Criteria for Predicting S^D Light Condition From Measurements of Parameters of Female Pulse Trains During S^D Reversal

	Steady	Flashing
Onset	< Md. overlap	> Md. overlap
Duration	> Md. overlap	< Md. overlap
Repetition Rate	> Md. overlap	< Md. overlap

The male's responses (left or right) to each dichotomized stimulus parameter alone and in combination with the other parameters are summarized in the contingency tables presented in Tables 15 through 19 for each calendar period, as there were some slight shifts in the distribution of the acoustic measurements over time. Table 20 presents an overall summary of Periods I - IV, but where cut-off points for the acoustic measurements obtained for the original calendar groupings are retained.

TABLE 15. Period I, S^D Reversal

Dichotomized Parameters of Female Pulse Trains										Total
Onset	None	<1.605				>1.605				
Duration	None	<2.205		>2.205		<2.205		>2.205		
Repetition Rate	None	<16	>16	<16	>16	<16	>16	<16	>16	
Paddle Response:										
Left	0	2	5	0	28	1	1	1	5	43
Right	0	7	0	3	5	20	10	1	3	49
Total	0	9	5	3	33	21	11	2	8	92

TABLE 16. Period II, S^D Reversal

Dichotomized Parameters of Female Pulse Trains										Total
Onset	None	<1.71				>1.71				
Duration	None	<2.105		>2.105		<2.105		>2.105		
Repetition Rate	None	≤18	>18	≤18	>18	≤18	>18	≤18	>18	
Paddle Response:										
Left	0	1	5	8	18	2	5	2	9	50
Right	0	3	3	6	6	24	3	3	4	52
Total	0	4	8	14	24	26	8	5	13	102

TABLE 17. Period III, S^D Reversal

Dichotomized Parameters of Female Pulse Trains										Total
Onset	None	<1.31				>1.31				
Duration	None	<1.62		>1.62		<1.62		>1.62		
Repetition Rate	None	≤16	>16	≤16	>16	≤16	>16	≤16	>16	
Paddle Response:										
Left	1	3	0	8	33	1	0	1	12	59
Right	11	4.5	3	6	1	22.5	9	2	1	60
Total	12	7.5	3	14	34	23.5	9	3	13	119

TABLE 18. Period IV, S^D Reversal

Dichotomized Parameters of Female Pulse Trains										Total
Onset	None	<1.59				>1.59				
Duration	None	<1.95		>1.95		<1.95		>1.95		
Repetition Rate	None	<19	>19	<19	>19	<19	>19	<19	>19	
Paddle Response:										
Left	0	1	2	7	17.5	2	0	1	2.5	33
Right	21	2	0	0	2	7	2	0	0	34
Total	21	3	2	7	19.5	9	2	1	2.5	67

TABLE 19. Periods I-IV, S^D Reversal

Dichotomized Parameters of Female Pulse Trains										Total
Onset	None	<Md.				>Md.				
Duration	None	<Md.		>Md.		<Md.		>Md.		
Repetition Rate	None	<Md.	>Md.	<Md.	>Md.	<Md.	>Md.	<Md.	>Md.	
Paddle Response:										
Left	1	7	12	23	96.5	6	6	5	28.5	185
Right	33	16.5	6	15	14	73.5	24	6	8	196
Total	34	23.5	18	38	110.5	79.5	30	11	36.5	381

TABLE 20. Predictions of Male's Performance Based on Individual and Combined Parameters of Female's Pulse Trains During S^D Reversal

Period	Predictions From Individual Parameters			Predictions From Paired Parameters			Predictions From All Parameters Combined	Obtained Performance
	Onset	Duration	Repetition Rate	Onset, Duration	Onset, Repetition Rate	Duration, Repetition Rate		
I	.720	.755	.745	.755	.825	.790	.850	.880
II	.640	.680	.710	.680	.710	.720	.730	.667
III	.750	.870	.760	.870	.765	.870	.880	.891
IV	.855	.895	.805	.910	.865	.895	.925	.896
I-IV	.730	.795	.745	.800	.750	.800	.820	.829

The prediction of performance success was based on the Goodman and Kruskal*** index of predictive association, λ_B , transformed so that the lack of any predictive association would equal 50% as in the present situation.

The resulting predictions of the male's performance success obtained from applying these statistical procedures to the measurements of the features of the female's signals agree, for the most part, to a most gratifying degree, with the actual performance success attained by the male. Although pulse train onset is generally the most distinctive of the parameters and the one most closely correlated with the S^D light mode (r_{pb} scores), it is generally the least successful pulse train feature in predicting the male's response. This is not surprising as the male's time base for an S^D period is 5.0 seconds longer (his only reference point for this discrimination is the onset of the Time In light) than that upon which the analysis is based, which would increase the difficulty of the discrimination of "early" versus "late" onsets. Pulse train duration is generally the most successful single predictor of the male's response, although in Periods I and II repetition rate was at least as good as duration.

***The Goodman and Kruskal index of predictive association (Journal of the American Statistical Association, 49, 1954, 732-764) for categorical data, λ_B , is a very straightforward measure of the proportional reduction in the probability of error in predicting a response (in this case) that is afforded by specifying one or more attributes of a stimulus. The index ranges from zero, no predictive association, to 1.00, complete predictive association. In terms of sample frequencies in a contingency table, we find

$$\lambda_B = \frac{\sum_j \max_k f_{jk} - \max_k f_{.k}}{N - \max_k f_{.k}}$$

where

f_{jk} is the frequency observed in the cell (A_j, B_k)

$\max_k f_{jk}$ is the largest frequency in column A_j

$\max_k f_{.k}$ is the largest frequency among the rows B_k .

or more simply

$$\lambda_B = \frac{\sum (\text{most frequent response to a stimuli} - \text{most frequent response})}{N - \text{most frequent response}}$$

In Periods I and II the combination of pairs of predictors are most successful when combined according to the lowest interparameter correlations, lower correlation indicating of course less redundancy in the acoustic attributes with respect to S^D condition. Therefore, when combined they carry more potential information to the extent that they independently exhibit a high correlation with the S^D light mode. Thus, in Periods I and II the combinations of onset with repetition rate and duration with repetition rate provide the most successful predictions of the male's response. In the two later periods, with the change in the female's signaling patterns towards omitting any pulse emissions in the flashing S^D condition, the predictive value of all parameters (including presence/absence of pulse emissions) is increased. In these periods, the pairing of either onset or repetition rate with the duration parameter yields the highest predictive efficiency (which in only one instance surpasses the value obtained for duration as a single parameter predictor).

The critical question is, of course, given the characteristics of all three parameters of any pulse train (including absence) to what degree of accuracy can the male's performance success be predicted. As is indicated in Table 20 the predictions based upon the combined characteristics of the three pulse train parameters agree very closely with the performance level attained by the male. On the assumption that the male's paddle response is exclusively determined by the above features of the female's signals it would be expected that over the 380 trials of Periods I - IV he would respond appropriately in 82% of the S^D periods; his actual level of success was only slightly above this (82.9%). In Period I there was quite clear evidence that this assumption was not met because the male's responses were at least partly controlled by the airborne tone bursts emanating from the control room. Consequently he would be expected to attain a higher level of performance than was predicted (88% obtained versus 85% predicted). Similarly, in the following period, with the elimination of the adventitious cues, the prediction based upon the female's signals would exceed the level of the male's performance (73% predicted versus 66.7% obtained). The prediction for Period III is essentially exact, while the prediction for Period IV is only slightly above his attained level due to an inexplicable drop in his performance during the first day of this calendar period.

PLAYBACK EXPERIMENT II

During Period V of the S^D reversal experiment virtually complete predictability existed between the female's reaction to the S^D light

(i. e. , she emitted at least one pulse train if the light was steady and was silent if the light was flashing) and the male's response to the female's phonations (or lack thereof). Therefore in preparation for the second playback experiment critical recordings (at 60 ips) were made during these sessions on the same equipment as previously used. Video recordings of the sessions were also obtained.

From these recordings forty S^D periods (twenty per light condition) were selected as playback stimuli on the same criteria utilized in the first playback experiment. The characteristics of the female's phonations selected as playback stimuli are presented in Table 21. It will be noted that she emitted a pulse train in all steady S^D periods, but pulsed in only four of the twenty flashing S^D periods.

TABLE 21. Characteristics of Pulse Trains Selected as Stimuli for Playback II

	Onset		Duration		Repetition Rate		N
	Mn.	S.D.	Mn.	S.D.	Mn.	S.D.	
Steady	1.44	0.84	2.55	1.03	23.6	4.4	20
Flashing	2.56	0.84	1.20	0.25	6.5	0.9	4

Preparation of the edited signals for the playback program followed the procedures used in the initial experiment. Sensing tape indicators, which marked appropriate points within a Time In period, were again used to control the experimental program via a photocell sensor which activated a stepping relay.

The signals were delivered into the water by a three element transducer. Each element delivered a frequency band so that with the appropriate cross-over network a relatively flat response from 2 - 100 kHz could be obtained. This transducer was placed in the female's enclosure approximately 5 feet in front of her light array and 2 feet in from the center barrier, as this was the position she occupied in the video recordings when she began her emissions.

The male was first worked in the playback (II) situation at the end of November, 1967. During this time problems with the programming equipment were still being encountered, therefore introducing extraneous sounds into the tank in conjunction with the Time In light onset. In addition, for the first 129 Time In periods, the gain on the power

amplifier driving the input transducer had been set at the same level that had been used at the end of the first playback experiment. Subsequently, this level was adjusted so as to obtain, for selected signals, the same peak-to-peak voltages from a pick-up hydrophone, which was suspended alongside the playback transducer, as had been recorded with this pick-up hydrophone originally. During these first 129 Time In periods, which derived from 64 steady and 65 flashing S^D conditions originally, the male pressed his left paddle in 90 (70%) instances and his right paddle in only 39 (30%) of the Time In periods. He responded correctly in only 57 (44%) of these trials.

As in the first playback experiment attempt, numerous problems with the equipment were encountered which interfered with steady progress in running this test. During the time required for corrections and repairs the animals were worked together. While the performance required of the male was unchanged during these sessions, the female was being forced to respond more rapidly in anticipation of the experimental situation which was to follow completion of the playback experiment.

It was not until mid-February, 1968 that the playback experiment could be resumed. At this time the programming equipment was functioning with consistent reliability and the amplitude of the input signals was comparable to that of the original signals. The loud transient clicks associated with all relay switches of the programming equipment were still (as in the first playback experiment) entering the water through the input hydrophone. Under the prevailing circumstances, however, the most favorable conditions in which the experiment could be conducted had been attained.

Over a two-day period two hundred Time In periods, equally divided between "steady" and "flashing" conditions, were presented to the male. During this time he was somewhat more likely to respond by pressing his right paddle (54%) than by pressing left (46%). This tendency was not, however, consistent across the five different presentations of the program. During the first 80 Time In periods he hit his right paddle only 23 (29%) times; while in the final 120 trials he hit right 85 (71%) times. It follows that his performance varied accordingly. Of the 33 correct responses in the first 80 Time In periods only 8 (24%) were in conjunction with a flashing signal, whereas in the following 120 trials 45 (69%) of the correct responses were to a flashing signal. The male's performance over all trials again failed to exceed the chance level, for he responded correctly in only 98 (49%) of the 200 Time In periods.

Although this second attempt to control the male's behavior with reproductions of recordings of the female's signals also failed perhaps because of the very noticeable switching transients that could not be suppressed, another signal reproduced over this system was found to have very marked, but untoward, behavioral effectiveness. This was a signal simulating the characteristics of the female's signals to the steady S^D light which was synthesized by filtering and attenuating a pulse series produced by a time mark generator. This was presented once to the male on 11 February after the male had gone through the whole program of 40 S^D periods several times. The synthetic signal was delivered at the same amplitude as the recorded signals, but some as yet unknown properties of the signal immediately provoked the male to extremely violent locomotor action, although he remained quite silent. No further tests with this signal have been performed because of this extreme behavioral reaction, although it would be interesting to determine what it is about this signal that produces this unexpected reaction.

ROLE REVERSAL EXPERIMENT

In order to obtain further information bearing on the basis of the animals' success in the previous tests of information transmission, a new condition has been imposed on their task. With everything else the same as in the S^D reversal experiment, the male is now required to transfer the critical environmental information to the female, rather than the other way around as in the prior tests, that is, the female is required to respond first, but the S^D light indicating which response is appropriate is only available in the male's enclosure. If their earlier success in transferring this information was due to the specialized development in these animals of a social signaling system whose referential scope is capable of accommodating the semantic requirements of our tests, then this communicative capacity ought to be available to the entire population and permit any one of them to transmit the information when the necessity arises. If, however, this pairs' earlier successes were due to particular features of their history of experience in this particular experimental setting, then, there would be no reason to expect easy interchangeability of their roles. That is, if the male and female together had each developed individual behavior patterns that enabled them to meet the demands of this task, the female coming to reliably produce acoustical signals in response to the S^D lights and the male coming to key his paddle responses to these signals in lieu of his diminished access to the S^D light signals, then these particular behavior patterns could not be appropriate to meet the changed experimental conditions.

The initial stage of the role reversal experiment involved training the animals to reverse the order of their responses. In all previous work the male had been required to respond first after which the female had been allowed 10 seconds to make her response. Under the conditions of role reversal the male would be presented with the S^D light, communicate the necessary information to the female, whereupon she would make her paddle response, and the male's response would follow.

A preliminary step in training began in February, 1968 when the animals were working together under normal (S^D reversal) conditions. During seven training sessions (involving 887 Time In periods) the female was forced to respond more rapidly by gradually decreasing the allotted amount of time for her response from 10 to 3 seconds following the male's response. During the final 180 trials the female's responses were all confined within a maximum interval of 3 seconds.

This preliminary work was followed by individually training the animals to reverse the order of their responses, i. e., female first, male last. In stages, the male was trained to delay his paddle response until the delivery (by the trainer) of the female's bridge signal, and the female was required to respond to her paddles without waiting for the occurrence of the male's bridge tone (delivered by the trainer). Each animal was worked until all responses occurred within a 10 sec interval required for each in the proper time sequence and an overall performance level of at least 90% was attained. The male required 696 trials, the female 246 trials, to reach these criteria.

The animals were first worked together in early March under the new conditions. As in all training involving new conditions, complete light arrays were placed on both sides of the tank (256 Time In periods with 85.9% correct). The male's light array was then gradually moved toward the female's side of the tank until it was next to her lights (over 170 Time In periods with 88.2% correct) when it was removed (90.9% correct over 132 Time In periods). The Time In light remained on the female's side as the S^D light was moved gradually toward its final position—centered between the male's paddles (75.5% correct over 466 Time In periods). The male's Time In light was reintroduced at this point and, because of a decrease in the female's performance, his complete light array was shifted toward the center barrier then back to its normal position (884 trials with 69.2% correct).

By the end of May, the termination of the contract period, the final disposition of the signal lights had been achieved, the male having both

a Time In and an S^D light in his enclosure, the female with only a Time In light on her side. Since then the curtain forming a visual barrier between the enclosure was gradually drawn across the tank at a rate determined by the maintenance of a 90% or better level of performance success. This permitted complete visual separation of the animals by the middle of July without decreasing performance levels.

However, the attained level of success had been achieved by a process that had also threatened to develop in the earlier work, with the female's development of a means of responding correctly by her discriminating, either by echo ranging or passive listening, the position of the male as he approached his paddles. This process has been demonstrated by reducing the distance between the male's paddles so that the difference in the male's position in his paddle approaches is reduced. The result of this change in the location of the male's paddles is a reduction in performance level, though because the male usually maintains fairly consistent differences in orientation in the two S^D conditions, the reduction in performance levels has not decreased below 70% correct.

Because of the development of the female's discrimination of the male's position as a substitute for the S^D light signal which is no longer available to her, the pair has not yet been completely exposed to the requirement for social signaling. However, by maintaining the male's paddles in their narrow positions or by their elimination, we plan to keep them exposed to the full demands for active information transfer by the male as long as required to achieve a satisfactory test.

Whatever the outcome of these tests, the results so far clearly indicate the lack of any easy interchangeability in the roles by which the animals had achieved their original success, thus, this is further evidence against the hypothesis that their prior success had been based on a social signaling capability that has developed in these animals which provides for the general ability to transmit information of the kind required. The final results of these tests will be reported in a future report.

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13. ABSTRACT An attempt was made to establish the critical signal characteristics of sounds emitted and received by a pair of bottle-nose dolphins during a test of their capacity to transmit information concerning the arbitrary features of their environment. The nature of the behavioral processes involved in the animals' emission and reception of these signals was also investigated. It was determined that the signals successfully used by the dolphins to transmit information were apparently the result of specific learning that occurred during the training period leading up to the actual information-transfer tests. There was no evidence to indicate (and much to contra-indicate) that the animals' performance success had derived in any direct way from their "normal" modes of social interaction.		

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